

SPECIES CRITERIA IN *ANGUISPIRA* (*ANGUISPIRA*)
(PULMONATA: DISCIDAE)

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ABSTRACT

The functioning surface of the penis in Anguispira (Anguispira) shows consistent differences in pilaster pattern among A. alternata (Say, 1816), A. cumberlandiana (Lea, 1840), and A. picta (Clapp, 1920), although the gross appearance of their genitalia is nearly identical. Investigation of the conchologically divergent morphs lumped as A. alternata probably will result in recognizing several species. The genital difference reported here corresponds with major shell shape and sculpture differences. Radular structure in the Discidae, as represented by Anguispira, is generalized and differs from the basic patterns found in the Charopidae, Endodontidae, and Helicodiscidae.

INTRODUCTION

The ribbed and unicolored to flammulated shells grouped as *Anguispira* and *Discus* have been monographed by MacMillan (1940) and Pilsbry (1948). Comparison of these papers shows considerable disagreement as to species limits and affinities, although the generic limits are the same. MacMillan (1940) relied strictly on the shell for taxonomic decisions and Pilsbry (1948: 566) indicated that "...fundamental inaccuracies are involved" in MacMillan's phylogenies. Preliminary work by H. B. Baker on the anatomy of various species of *Discus* was included by Pilsbry (1948: 599-600) in the form of a key, together with some anatomical details on both *Anguispira* (*A.*) *alternata* (Say, 1816) and *A.* (*Zonodiscus*) *kochi kochi* (Pfeiffer, 1845) (Pilsbry, 1948: 568, fig. 304), and, additionally, *Discus* (*D.*) *patulus* (Deshayes, 1830) (Pilsbry, 1948: 599, fig. 327). Subsequently Forcart (1957) commented on the subgeneric divisions of *Discus*; Umiński (1962) revised the Palearctic species of *Discus* and summarized the widely scattered European literature; and Umiński (1963) reported on the anatomy of *Discus marmorensis* H. B. Baker, 1932.

Various discrepancies and contradictions in these accounts will be discussed elsewhere (Solem, *in preparation*). Here, it is sufficient to point out that the species of *Discus* have

several longitudinal pilasters within the penis (Pilsbry, 1948: 599, fig. 327a; Umiński, 1963: 84, figs. 5-8) and in *Anguispira* there are only two pilasters, one very large and the other small (Pilsbry, 1948: 568, figs. 304C, 304F). There has not been any detailed study of the anatomy in different species of *Anguispira* previously, and unpublished observations by Hubricht, Grimm and myself had failed to identify species level identification features from the external aspects of the genitalia.

During a survey of rare and potentially endangered land snail species of Eastern North America for the Office of Endangered Species, it was necessary to investigate the status of the taxa grouped as *Anguispira* (*A.*) *cumberlandiana* (Lea, 1840). MacMillan (1940: 392-394) and Pilsbry (1948: 586-589) recognized four subspecies, *A. c. cumberlandiana* (Lea, 1840) from Northeastern Alabama and Tennessee; *A. e. alabama* (Clapp, 1920) from Northeastern Alabama; *A. c. columba* (Clapp, 1920) from Marion Co., Tennessee; and *A. c. picta* (Clapp, 1920) from near Anderson, Franklin Co., Tennessee. Clapp (1920) described *Anguispira picta* as a full species, and Hubricht (unpublished) agreed with this opinion on the basis of shell features.

This paper reports on species level differences in the terminal genitalia of *Anguispira*

(*Anguispira*) *alternata*, *A. cumberlandiana*, and *A. picta*, and thus suggests features that can be investigated to determine the status of the many forms that have been lumped as *A. (A.) alternata* by earlier authors and Pilsbry (1948), but split into several species by Hubricht (1952, 1965, 1968, 1970, 1974) on the basis of field observations and shell features. Radular teeth of the same three species are illustrated to show the basic structures and inter-row support mechanisms of the central and lateral teeth in the Discidae.

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MATERIAL STUDIED

The data on the illustrated material are as follows:

Anguispira (A.) alternata (Say, 1816). Northwest side of Route 272, 0.4 miles southwest of Route 270 junction, north side Rich Mountain, Polk Co., Arkansas. Glenn Goodfriend! September 13, 1973. Field Museum of Natural History 176186.

Anguispira (A.) cumberlandiana cumberlandiana (Lea, 1840). Near Martin Springs Road, 8 miles south of Monteagle, Marion Co., Tennessee at 960 feet elevation. Glenn Goodfriend! September 4, 1974. FMNH 171433.

Anguispira (A.) picta (Clapp, 1920). Southwest side of Buck Creek Cove, 4 miles south of Sherwood, Franklin Co., Tennessee at 750 feet elevation. Glenn Goodfriend! September 6, 1974. FMNH 171138.

Several additional sets of typical *A. alternata* were dissected, but are not illustrated, since

they agreed with the structures seen in the figured material. What appears to be seasonal variation in the prostate-uterus and development of the main pilaster was discovered. Material collected at the same time of year was selected for illustration, despite the geographic incongruence of the *A. alternata* set.

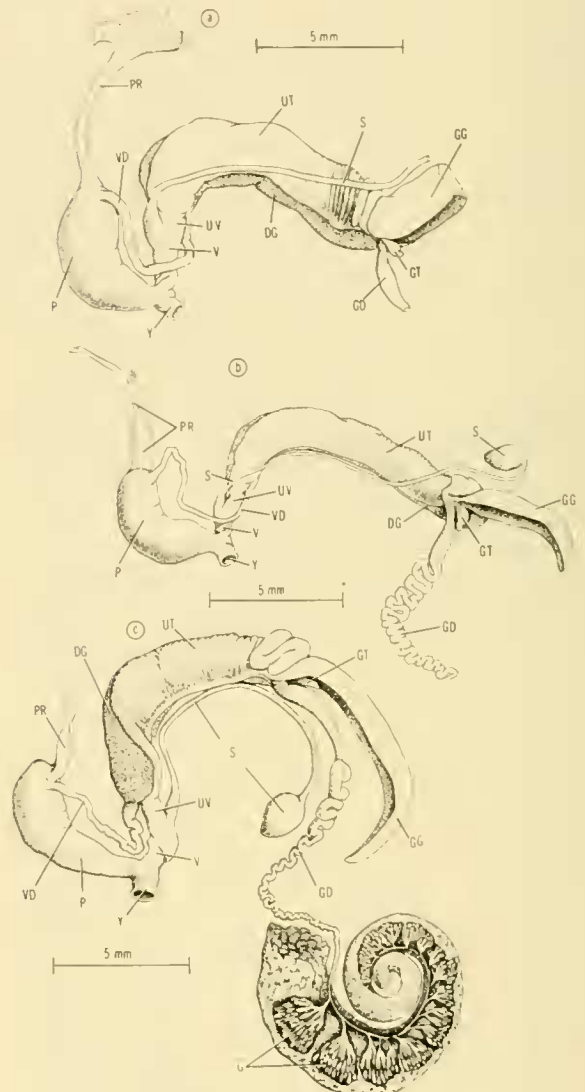


FIG. 1. Genitalia of *Anguispira*: a, *Anguispira alternata alternata* (Say, 1816). FMNH 176186. North side of Rich Mt., Polk Co., Arkansas; b, *Anguispira picta* (Clapp, 1920). FMNH 171138. Buck Creek Cove, south of Sherwood, Franklin Co., Tennessee; c, *Anguispira cumberlandiana cumberlandiana* (Lea, 1840). FMNH 171433. About 8 miles south of Monteagle, Marion Co., Tennessee. Scale lines equal 5 mm.

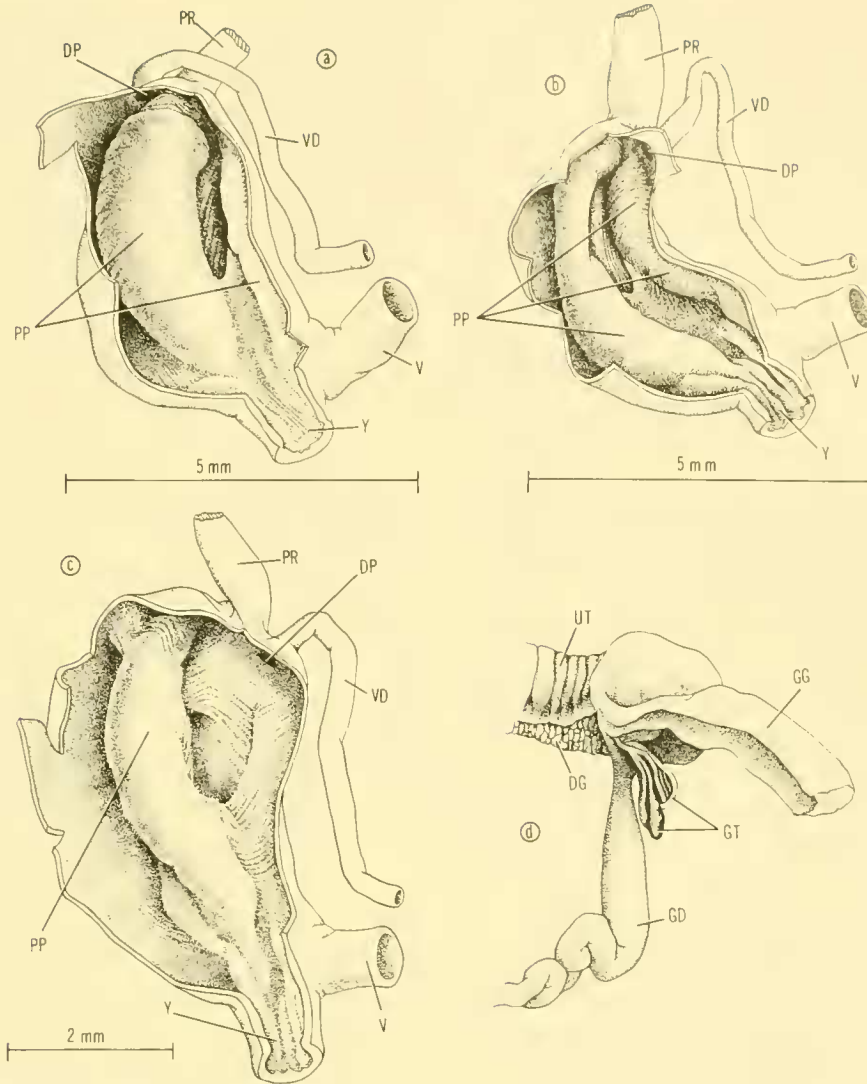


FIG. 2. Penis internal structure and talon in *Anguispira*: a, *Anguispira alternata alternata* (Say, 1816); b, d, *Anguispira picta* (Clapp, 1920); c, *Anguispira cum-*

berlandiana cumberlandiana (Lea, 1849). Scale lines as marked, d greatly enlarged.

TERMINAL GENITALIA

The apical genitalia of *A. alternata* and *A. picta* are not illustrated, since the ovotestis (G) and hermaphroditic duct (GD) showed no differences from the structures seen in *A. cumberlandiana* (fig. 1 c). All three species have the tri-lobed talon (fig. 2 d, GT) first reported by Pilsbry (1948: 568, fig. 304D). *A. picta* (fig. 1 b) does have a slightly longer prostate (DG) and uterus (UT), but this may be a facet of individual population variation. The very long

spermatheca (S) and slender, fingerlike albumen gland (GG) also are typical of the Discidae. *A. alternata* (fig. 1 a) does have a shorter free oviduct (UV) than either *A. picta* (fig. 1 b) or *A. cumberlandiana* (fig. 1 c). There is a slight variation in the length of the vagina (V), but because of the angle at which the spermatheca joins the free oviduct to form the vagina, measuring the exact length of the latter is very difficult.

In all *Anguispira* (*Anguispira*) examined so

far, the vas deferens (VD) emerges abruptly from the acini bundles of the prostate, narrows slightly and lies free of the adjacent tubes in its passage to the peni-oviducal angle, then reflects apicad to enter the penis (P) through a simple pore (fig. 2 c, DP). The vas deferens entrance is lateral to insertion of the penial retractor muscle (PR), which, contrary to previous literature statements, arises from the diaphragm, not the columellar muscle. In all cases the insertion of the penial retractor muscle is on the apex of the penis. The illustration of *A. cumberlandiana* (fig. 1 c) suggests that the insertion is slightly lateral instead, but this is an artifact of preservation. The illustrated specimen was partly retracted into the shell. As part of the retraction process, the penis is shifted apicad relative to the origin of the penial retractor muscle. At full shift the apex of the penis is bent slightly to the left and the retractor muscle extends diagonally anteriorly, rather than in its normal apical orientation. When fixed in the preservative, this slight distortion can be misinterpreted as part of the basic structure unless it is compared with the condition found in fully expanded materials.

There is a definite difference in the shape of the penis, which is caused by the quite divergent internal pilaster structures (figs. 2 a-c). In *A. cumberlandiana* (fig. 1 c) the penis tapers almost evenly from apex to atrial junction (Y). In *A. picta* (fig. 1 b) the penis has an almost uniform diameter on its upper two-thirds, then rapidly narrows toward the atrium on its lower third. *A. alternata* (fig. 1 a) has a more bulbous penis that narrows slightly apically, but tapers toward the atrium on its lower two-fifths. Typically these differences can be detected, but flattening during dissection or in the initial preservation process can distort individual specimens and mislead the observer.

Only by slitting the penis from atrium (Y) to penis pore (DP) and studying the major pilasters, can the differences (fig. 2) be seen clearly and the species differentiated without question. In *A. alternata* (fig. 2 a) the major pilaster (PP on left) expands to great size, tapers very slightly at the apex, and sharply near the atrium. The second pilaster (PP on

right) is a narrow, much lower, raised ridge that varies at most slightly in height over its entire length. In *A. picta* (fig. 2 b) the major pilaster (PP) expands much less, even on its lower third, then narrows greatly toward the middle, and is a relatively narrow ridge in its upper half. The second pilaster is lower, wider on its lower half, then broadens into a semicircular pilaster on its upper half. The second pilaster itself is composed of less dense tissue. In *A. cumberlandiana* (fig. 2 c) the main pilaster is rather high and narrow, without major size change from near the apex to near the atrium. The second pilaster is greatly reduced in height, becoming a wide, nearly flat patch of fibrous tissue. Near the middle of the penis in each species, a "pocket" is formed by a flap of tissue running between the two pilasters. This is vaguely similar to a structure found in many Charopidae, but apparently formed quite differently (Solem, unpublished). All *Anguispira* have vague longitudinal fold ridges extending from the atrium into the penis base (figs. 2 a-c). One or two of these may extend up alongside the major pilaster, but I have not dissected enough individuals to determine if the longer ridge shown for *A. cumberlandiana* (fig. 2 c) is an individual variation or represents another species difference. The different shapes found in the two large pilasters are characteristic within quite narrow limits and thus represent species differences.

The above observations are based on studying five individuals from each population, and on sampling ten populations from the Middle West and Eastern United States of *A. alternata*. The differences in pilaster structure are constant and I conclude that they are valid species differences. Thus *A. picta* is distinct from *A. cumberlandiana*, as originally proposed by Clapp (1920), and both are distinct from *A. alternata*. Restudy of dissections that I had made many years ago of *A. fergusonii* (Bland, 1861) from Cambridge, Maryland, (specimens courtesy of Ralph Jackson), *A. macneili* Walker, 1928 from Alabama (specimens courtesy of Leslie Hubricht), and new dissections of *A. mordax* (Shuttleworth, 1852) from Well Spring, Campbell Co., Tennessee (FMNH 137820, L. Hubricht! June 5, 1964) show equally different

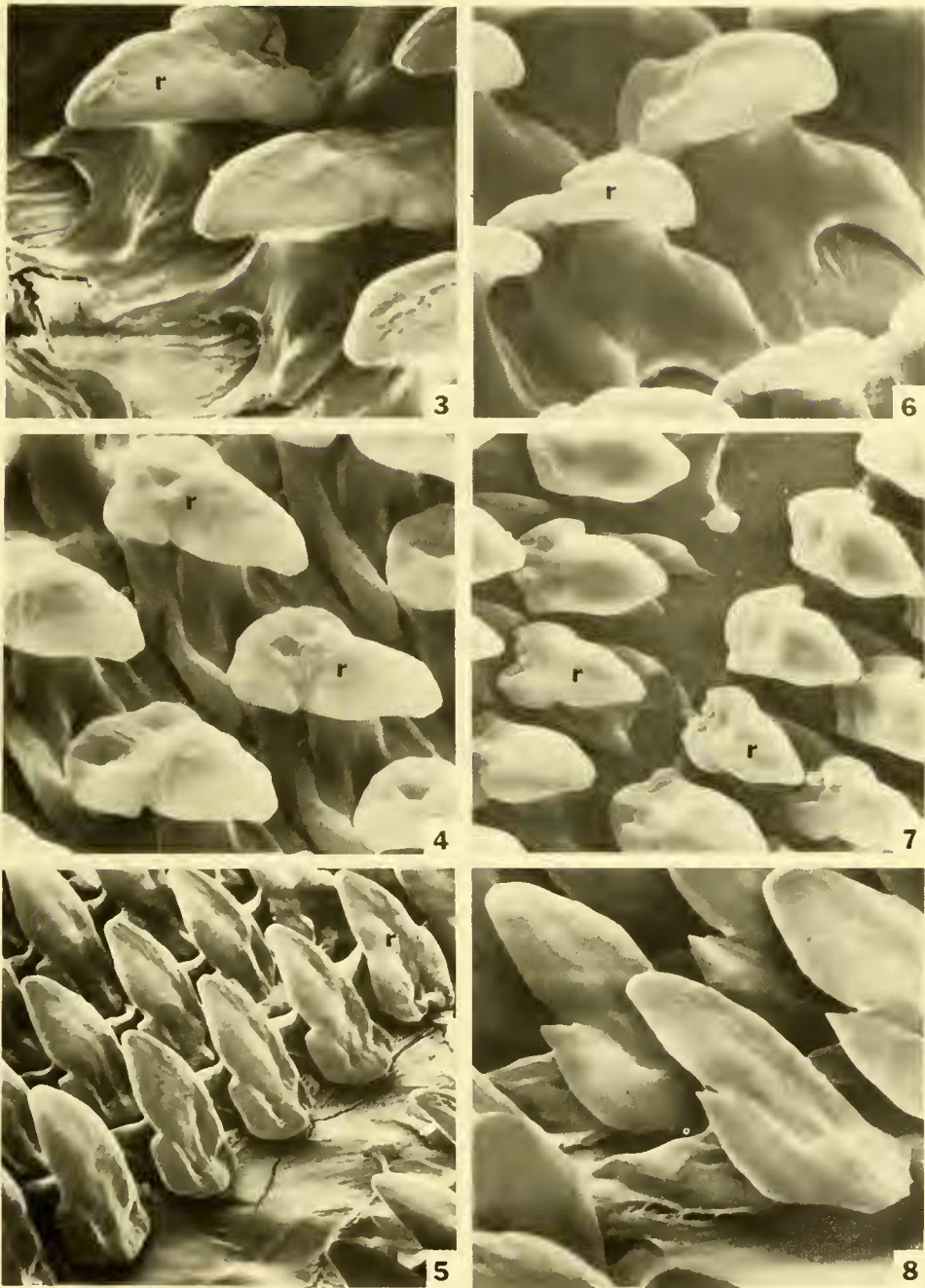
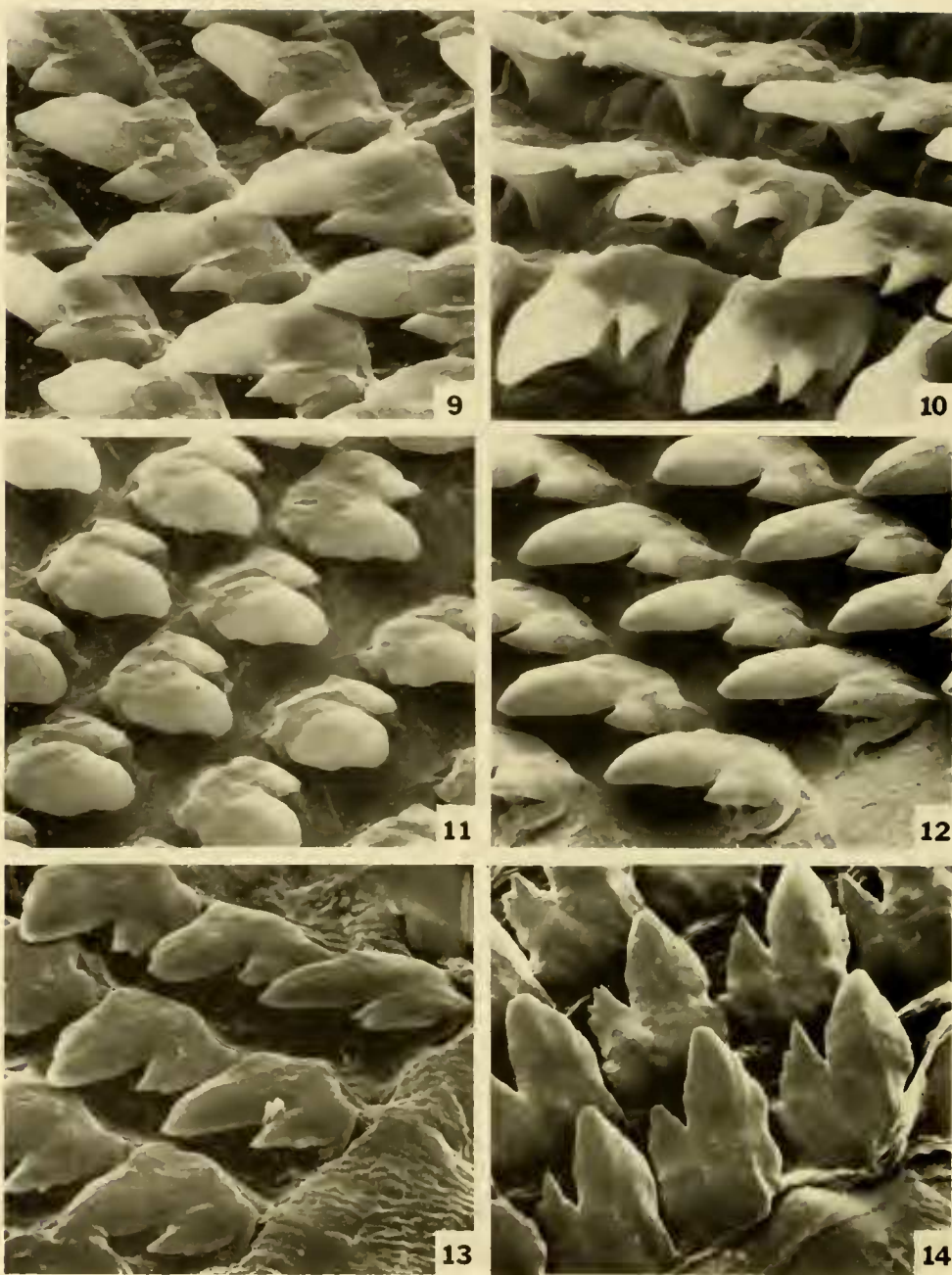


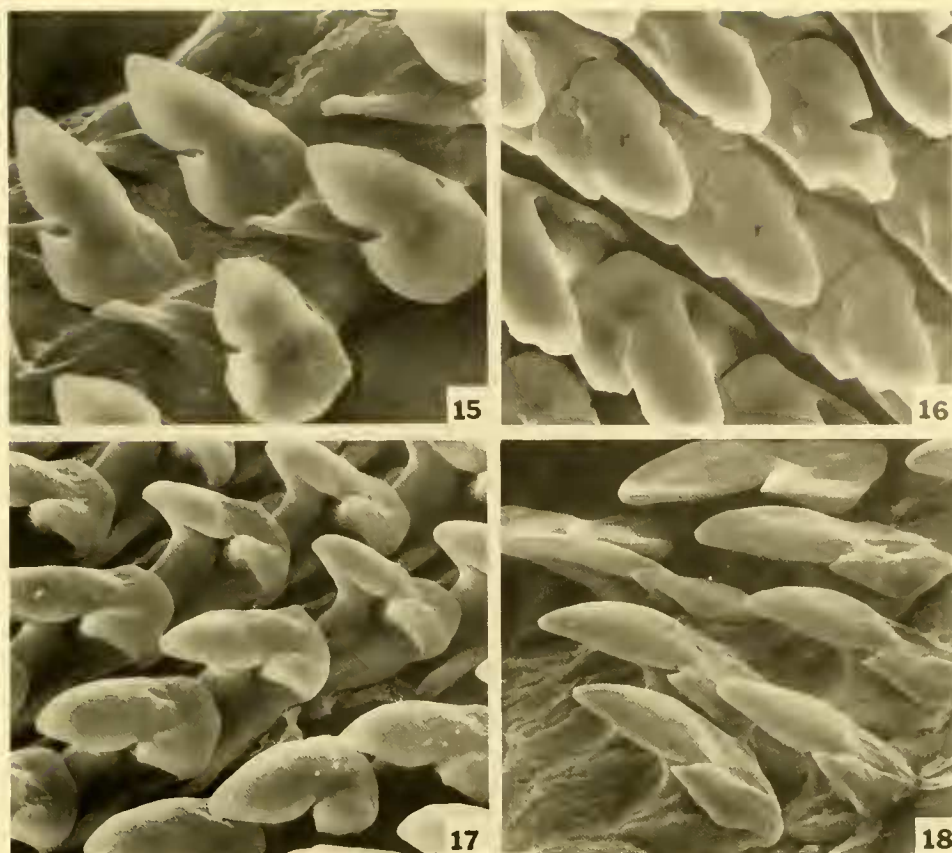
FIG. 3-8. Central and lateral radular teeth. Figs. 3-5, 8. *Anguispira picta* (Clapp, 1920). FMNH 171138. Fig. 3. Newly formed central (upper center) and 1st lateral teeth. 1,135 \times . Fig. 4. Lateral teeth from mid section of radula showing functioning of support ridge and anterior flange. 1,260 \times . Fig. 5. Central (upper right) and lateral teeth viewed from anterior angle, erected position. 650 \times . Fig. 8. Late lateral tooth viewed from low outside angle to show

extent of free anterior margin. 1,315 \times . Figs. 6-7. *Anguispira cumberlandiana cumberlandiana* (Lea, 1840) Fig. 6. Central (left) and 1st lateral near posterior end of radula showing dual support ridges on central, single support ridge on lateral, marked anterior flange of lateral. 1,250 \times . Fig. 7. Central and early lateral teeth viewed from a high posterior angle. 650 \times .



FIGS. 9-11. *Marginal rudular teeth*. Figs. 9-10. *Anguispira alternata alternata* (Say, 1816). Fig. 9. Outer marginals from high posterior angle. 1,300 \times . Fig. 10. Outer marginals on a creased area to show shape and angle of elevation. 1,300 \times . Fig. 11. *Anguispira cumberlandiana cumberlandiana* (Lea, 1840). FMNH 171433. *Submarginal teeth*

from a high central angle. 625 \times . Figs. 12-14. *Anguispira picta* (Clapp, 1920). FMNH 171138. Fig. 12. Transition from lateral to marginal teeth. 1,000 \times . Fig. 13. Outermost marginals showing splitting of side cusps. 1,250 \times . Fig. 14. Outermost marginals from a high anterior angle. 1,115 \times .



FIGS. 15-18. Radular teeth. Figs. 15-17. *Anguispira alternata alternata* (Say, 1816). FMNH 176186. Fig. 15. Newly formed early lateral teeth showing function of basal support ridge. 1,050 \times . Fig. 16. Worn central and early lateral teeth from anterior end of radula. 1,000 \times . Fig. 17. Lateral teeth.

1,160 \times . Fig. 18. *Anguispira picta* (Clapp, 1920). FMNH 171138. Transition from lateral to marginal teeth showing shortening of basal plate and reduction of anterior flare. 1,110 \times .

pilaster patterns in these taxa. Revision of the *Anguispira alternata* group is beyond the scope of this study, but the existence of distinctive pilaster patterns in some of its more strongly characterized "races" indicates that several species are represented, as Hubricht has suggested previously on the basis of his collecting experiences. An investigation of penis pilaster structure in this complex can be expected to yield significant data, despite the lack of obvious differences in the gross genitalia.

RADULAR STRUCTURE IN *ANGUISPIRA*

The radulae were prepared using the techniques outlined in Solem (1972). Published illustrations have been chosen to demonstrate the functioning and structure of the inter-row support system in the Discidae, to illustrate the

pattern of change from lateral to marginal teeth, and to demonstrate the form of the marginal teeth. Differences between the three species are trivial, with *A. cumberlandiana* (fig. 7) having a smaller central tooth in relation to the 1st laterals than either *A. picta* (fig. 3) or *A. alternata* (fig. 16) and *A. alternata* (figs. 15-17) having a more prominent ectocone on the lateral teeth than either of the other species.

The rachidian or central tooth of the radula, marked "r" in figs. 3-7 and 16, has very weak to weak ectocones, a variably (fig. 7) indented and sinuated anterior margin, no anterior flare, and two prominent lateral buttresses on the basal plate (figs. 3, 6, 7). The first lateral teeth are immediately recognizable in that they lack an endocone (fig. 7) and in having the basal plate buttress only on the outer side of the

basal plate (fig. 6). In addition, there is a distinct anterior support flare on the early laterals that is lacking in the rachidian tooth (fig. 5). When a tear in the basal membrane partly separates two rows of teeth (figs. 5-7), then the basal plate structures and anterior flares can be observed quite easily. After the first few lateral teeth, the basal flare becomes accentuated and somewhat elongated (fig. 8), with the anterior two-fifths of the tooth free of the basal membrane. This is the generalized "helicoid" pattern for inter-row support of the laterals (see Solem, 1972; pl. 5, figs. 22-23). Figs. 3, 4, and 7 show the stress support system in various phases of operation. For the rachidian tooth, the anterior margin is pressed back against the basal plate and fits right in between the lateral buttresses. Fig. 7 shows two stages in the process: at far left, the anterior flare is tilted down, but not in contact with the basal plate, while at far right the flare is in contact. Fig. 16 shows the interlock system in full operation even more clearly. The first lateral teeth differ only in the stronger anterior flare being pressed partly against the shaft of the cusp and partly against the outside buttress (lower left of fig. 4 and center of fig. 15).

This is a highly generalized buttress system that is widely distributed in the Pulmonata and yields no information as to the phylogeny of the group.

Transition from lateral to marginal teeth occurs fairly abruptly (figs. 17-18) and involves changes in basal plate, anterior flare, cusp length, and angle at which the cusp is pointed. Fig. 17, top to bottom, shows the shortening of the anterior flare, while the different angle in fig. 18 demonstrates the further progression in this loss and the then very rapid change in the length of the posterior section of the basal plate. The shift is completed with the teeth at the bottom of fig. 18, where the anterior margin is simply rounded, the cusp is at a lower angle, the posterior section of the basal plate is greatly shortened, and the lateral buttress on the basal plate is lost. The shift in angle of the cusp continues to the point shown in fig. 12, where the cusp is elevated a comparatively few degrees from horizontal. At this point, a weak endocone may appear on some of

the marginals, although most (fig. 11) will have only a small knob-like protrusion. Newly formed marginals (figs. 9, 10) in *A. alternata* show no special features, but fig. 10, which was taken at a curve in the radula, effectively demonstrates the cusp angle. Outermost marginal teeth (figs. 13, 14) show irregular splitting of the ectocone with teeth in successive rows showing different ectoconal splitting features. In some individual outer marginal teeth there is a weak endocone (upper right of fig. 14).

In maintaining a basically bicuspid condition, the lateral and marginal teeth of the Discidae differ from those of the Charopidae (Solem, 1974: 167) or Helicodiscidae (Solem, 1975: figs. 6-8) which are essentially tricuspid with often extreme cusp splitting. The Endodontidae (Solem, 1973: figs. 6-9, 13-14) also have bicuspid lateral teeth with bicuspid to tricuspid marginals, but the inter-row support system (*loc. cit.*, figs. 6, 14) is very different. The anterior margin of the lateral teeth is rounded and totally lacks an anterior flare, the cusps are narrower and curved, and support comes by pressing against the raised posterior tip of the basal plate ridge. When viewed with optical equipment, the endodontid and the discid radulae would look essentially identical, but the functioning patterns in the two groups are very different.

SHELL FORM AND GROSS SCULPTURE

Differences in shell form and sculpture between the nominate taxa of the three species have been covered quite adequately by Mac-Millan (1940) and Pilsbry (1948). *Anguispira alternata* (Say) has a rounded to angulated periphery on the body whorl and weak to very strong radial ribs that continue across the periphery and into the umbilicus. *A.umberlandiana* (Lea) has a protruded, thread-like peripheral keel with prominent radial ribs that continue across the keel. *A. picta* (Clapp) has the radial ribs present on the upper spire, but absent from the body whorl and with the protruded peripheral keel smooth and without any trace of radial ribbing.

Because races of *A. alternata* and *A.umberlandiana* vary greatly in the prominence of their sculpture, considerable uncertainty con-

tinues to exist concerning the limits to be assigned sculptural variation within a species. Thus the decisions by MacMillan (1940) and Pilsbry (1948) to combine *A. picta* with *A. cumberlandiana* were based on the latitude of sculptural variation in the morphs lumped as *A. alternata*. The demonstration here of differences in the penial pilaster patterns between *A. picta* and *A. cumberlandiana* suggests that investigation of the named forms of *A. alternata* that show widely divergent sculpture may lead to a splitting of that taxon into several discrete units.

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RANGE EXTENSION OF *CORALLIOPHILA MARRATI* KNUDSEN (GASTROPODA: MAGILIDAE)

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ABSTRACT

Coralliophila marrati Knudsen, 1956 originally described from off Liberia is here reported from Congo and Angola.

In his report on the molluscs collected during the *Atlantide* Expedition to the coasts of tropical West Africa, Knudsen (1956) described three new species of the family Magilidae: *Coralliophila jarli*, *C. kraemmeri* and *C. marrati*. Although all were based on one or two specimens, no doubt seems to exist concerning the specific status of these species.

Coralliophila marrati was based on a single specimen dredged from a depth of 78 m at 5°

06' N, 9° 34' W off Liberia. Since Knudsen's description no additional data have been added to the distribution of *C. marrati*.

The Zoological Museum of Amsterdam acquired the second known specimen from Mr. W. Bergmans. This specimen was collected in 1969 by J. Moret near Pointe Noire, Congo. It agrees in full detail with the original description of Knudsen (1956: 29, pl. 2, fig. 14). It is only slightly larger: height 26.7 mm; width 17.1